

PREY SELECTION IN AN ORB-WEAVING SPIDER:
MICRATHENA GRACILIS (ARANEAE: ARANEIDAE)*

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INTRODUCTION

A number of studies have examined the prey captured by web building spiders, and many have compared the captured prey with the insects available in the environment (Bilsing 1920; Turnbull 1960, 1962; Cherrett 1964; Kajak 1965; Olive 1980; Nentwig 1980, 1983; Brown 1981; Shelly 1983, 1984; Robinson & Robinson 1970, 1973; Riechert & Tracy 1975; Uetz et al. 1978; Chacon & Eberhard 1980; Uetz & Biere 1980; Riechert & Cady 1984). The most common comparisons are between prey found in webs and the "potential prey" captured by traps that in some way mimic spider webs (sticky traps, windowpane traps, etc.). Although there is disagreement about what kind of trapping method most accurately assesses the prey actually available to spiders (see Uetz & Biere 1980; Chacon & Eberhard 1980; Shelly 1984), all these studies suggest, to a greater or lesser extent, that the range of prey taken by spiders demonstrates some degree of selectivity. Recent research has shown that specialization is the result of web placement, web structure, and behavioral choices in the attack process (Chacon & Eberhard 1977; Uetz & Biere 1980; Riechert & Luczak 1982; Nentwig 1983; Shelly 1983, 1984; Riechert & Cady 1984; Craig 1986; Stowe 1986).

An important question that many of these studies have addressed concerns the role of the spiders' web in the selection of prey, and why some prey insects are trapped more or less efficiently than others. Most workers agree that the process by which insects fall prey to spiders in their webs is neither random nor passive because insects vary in their ability to avoid webs, or escape from them once caught (see Nentwig 1982; Craig 1986); and web design and function favor capture of specific prey types and sizes (see Riechert & Luczak 1982; Rypstra 1982; Stowe 1986). The capture of insects by spiders on the

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web is also a non-random process; i.e., spiders have the ability to choose whether or not to attack, ignore or reject prey caught in their webs. Behavioral choices made by spiders at this level of contact are made on the basis of prey size, activity, and palatability (Riechert & Luczak 1982; Shelly 1983, 1984). Here, we examine the prey capture process in a common orb-weaving spider, and demonstrate selectivity at several levels.

STUDY SPECIES

Micrathena gracilis is a common orb weaver (Araneidae) occurring in the Eastern deciduous forest region of North America (Levi 1985). *Micrathena* occurs solely in large open spaces in the forest understory, where it is exposed to a diversity of flying insect prey. *M. gracilis* builds a small (20 cm diameter) orb within a relatively large frame (often 1.5–2 meters across). This suggests that these spiders have a large energetic expense in their webs, but should have a low encounter probability for all but the most abundant of prey. In addition, *Micrathena* is slow moving and almost clumsy, and usually takes > 3 sec. to reach a prey item in its web. Since most insects can escape entanglement in that time (Nentwig 1982), prey capture efficiency should also be low. This species is thus uniquely suited to provide a conservative test of the null hypothesis of no prey selectivity, because its characteristics suggest that opportunistic predation and extreme generalization of diet are an appropriate strategy.

In an earlier study (Uetz & Biere 1980), the prey caught in several types of web-mimicking traps (windowpane, sticky screen, artificial sticky web) and in a sweep net were compared with prey captured by spiders. It was clear from these data that *M. gracilis* were not taking prey in the proportions encountered. The spiders appear to capture larger flies and hymenopterans at far greater frequencies than they are potentially available. Artificial sticky webs, similar in size and with thread density identical to *M. gracilis*, were hung in the forest next to live spiders. For several days, the insects that flew into and escaped from the natural and artificial webs were noted from an observation post nearby. Both webs retained a different size array of insects than they encountered, and from this array, spiders selected only the largest insects (Uetz & Biere 1980). These preliminary studies suggested that *M. gracilis*, contrary to predictions based on its habits, might be a prey size specialist, and so this study was conducted.

METHODS

The study sites were located in Mount Airy Forest and Felter's Tanglewood, two deciduous ravine forest city parks in Cincinnati, Ohio. Both woods were characterized by a high, patchy canopy and a variable understory of shrubs, saplings and wide open spaces between vegetation. The dominant tree species were *Acer saccharum*, *Quercus alba*, and *Fagus grandifolia*. The two study sites were very similar in their physiognomy and were located within 3 km of one another. Two sites were chosen in order to minimize any vegetational disturbances that might occur during the course of the study due to the placement of artificial sticky web traps in the understory vegetation.

Because of potential bias in sampling insects found in spiders' webs, prey preference in orb weavers is best studied by examining the fate of insects that encounter the web. Observation of *Micrathena* in the field allows a comparison of the prey captured by the spider with potential prey items made available to the spider by its web within the forest understory. Because the spider was present, these observations allow a test of the null hypothesis of no selectivity: that *Micrathena* actively attacks all types and size classes of insects sticking to its web in proportion to the rate at which they are encountered.

Adult female *Micrathena* were observed for a total of 77 web hours (No. of webs \times hours observed) between 1 August and 10 September 1981. After locating the web(s), the observer sat on a stool 1 to 1.5 m from the web(s). This distance allowed close observations of even the smallest insects striking the web, but was far enough away not to disturb the spider. Observations took place during the normal diurnal activity period for this species, between 0800 hrs and 1800 hrs, and lasted from 1 to 2 hours at a time. Up to three webs could be observed at once if they were clumped within 1 to 2 m of one another.

When an insect struck the web, its length (estimated by holding a mm scale close to the web) and taxon were recorded. The insect's "fate" in the web was then followed. (It should be noted that the "fate" of insects already present in the web at the beginning of the observation period was not recorded. This was done in order to prevent over-estimating the number of small insects that actually came in contact with webs (i.e. larger insects may have contacted the web and escaped—while the smaller ones were trapped and remained in the web—and the observer has no way of knowing the former unless he or she was present). An insect that struck any part of the orb was

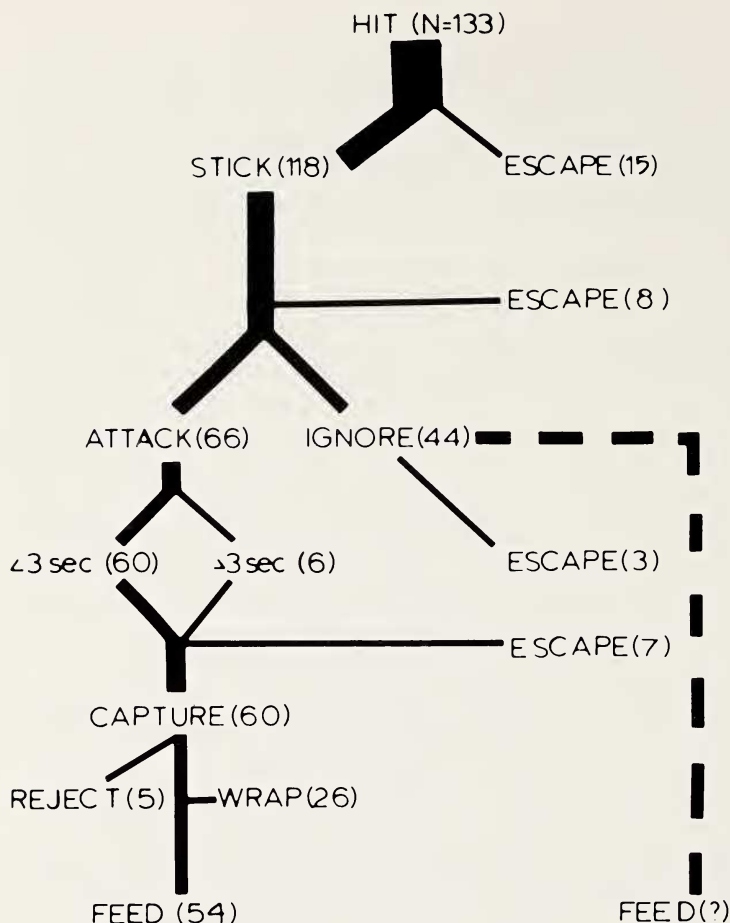


Figure 1. The predation sequence of *Micrathena gracilis*.

recorded as a HIT. An insect that was retained by the web longer than 3 seconds was called a STICK (after Rypstra 1982). Any insect that left the web at any time under its own power was termed an ESCAPE. An escape could occur at a number of different points along the predation sequence (see Fig. 1). An ATTACK occurred if the spider came in contact with the insect, usually with its two front legs. An IGNORE was recorded when the spider made no contact with the insect even

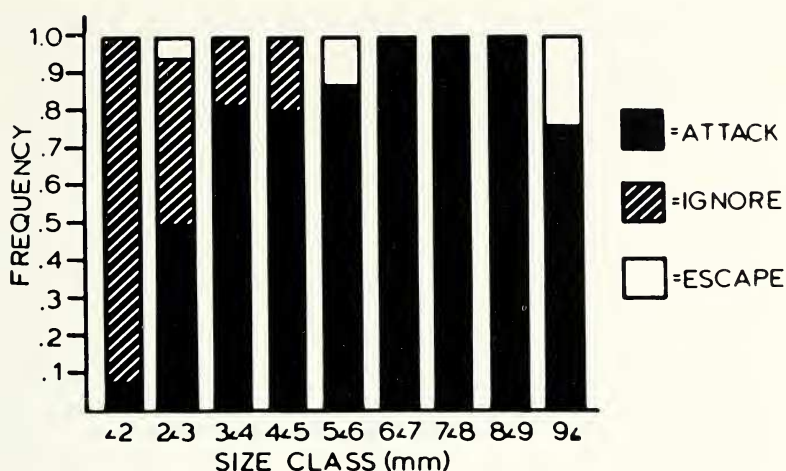


Figure 2. Size frequency distribution of insects attacked or ignored by spiders, showing the increased frequency of attacks on larger sized insects. Escapes shown occur after the 3 second "stick" criteria.

though it may have oriented toward and plucked at the insect in the web. A CAPTURE was recorded when the spider actually had control of the insect in its chelicerae. If the spider voluntarily discarded the insect, a REJECT was recorded. If the spider wrapped the prey item in silk after capture, a WRAP was recorded. Finally, if it fed on the insect during the observation period, a FEED was entered.

A comparison was also made of the insects captured by the web and those captured by a web-mimicking artificial sticky web trap (ASW) modified from a design reported by Uetz & Biere (1980). ASW trap frames were constructed out of 3/8 inch by 3/4 inch aluminum window screen frames (Custom Aluminum Products, Cincinnati, Ohio), with an area slightly larger than *M. gracilis* webs (38 cm × 38 cm). Clear, monofilament nylon thread woven onto a wooden loom surrounding the frame was held in the grooves of the window screen frame with spline in order to permanently secure the thread to the frame. This clear thread was 0.2 mm in diameter and could be woven into any desired mesh size. The mesh sizes used closely approximated those of *M. gracilis* (1 to 2 mm between

threads). Parallel threads representing radii were spaced 6 mm apart and perpendicular to these other threads (woven parallel 1–2 mm apart). The threads of each ASW were covered with equal amounts of adhesive (Stick'em Special TM Sea Bright Enterprises) the night before they were placed in the field. The traps were transported to and from the field in reinforced cardboard boxes with dividers to keep webs from touching one another.

In the field, frames were suspended on sturdy string with centers at 1.50 m high in microhabitats similar to these exploited by *M. gracilis*. Traps were placed in the field seven times, on nonrainy days between 23 July 1980 and 14 September 1980 (four times in Mt. Airy Forest and three times in Felter's Tanglewood). They were in place by 0730 hrs (while spiders were actually building their webs) and removed by 1900 hours (when spiders began taking down their webs). Care was taken in moving throughout the study sites so as not to destroy the vegetation of the microhabitats; two study sites were chosen in order to keep this problem to a minimum. Temperature and humidity were recorded on a Hydrothermograph placed in the center of the study site. Wind speed and direction were recorded only for the first two dates because wind was found to be negligible within the understory (also see Biere & Uetz 1980).

Traps were taken to the laboratory, where the insects were removed (by individually placing a trap in a large porcelain pan containing pure kerosene). This dissolved the adhesive and facilitated the removal of even the smallest insects. After the insects were removed and placed in labeled vials, the screen was cleaned by blowing the kerosene off with an air hose, rinsing it under hot water, air-hosing the water off, wiping the frame dry, and then placing the screen on absorbent paper for at least four days. No odor of kerosene could be detected at this point and further applications of adhesive stayed on with no apparent problems, so we felt confident in the re-use of traps. Insects were identified to order and their length was recorded with a micrometer to the nearest 0.5 mm.

The visibility of ASW's is a potential problem with their use, but we minimized this effect by using clear, nylon thread and a large frame size. Besides functioning in the same way as real webs, ASW traps have advantages over other sampling techniques that add to their usefulness in the field. Primarily, they allow an air-flow that is not

present in window-pane traps, which probably affects the accuracy of the latter (Robinson and Robinson 1970).

The design of our ASW's differs from that of previous studies in construction, area, mesh structure, and thread thickness. In comparison to Chacon and Eberhard (1980), ours more closely resembled the structure of actual spider webs, due to the presence of "radii", and thread thickness of 0.22 mm, (theirs was nearly 1.0 mm thick). This reduced the visibility of traps, an especially important consideration when studying diurnal orbweavers. Even though the "radii" of our traps were sticky, we believe that their presence is important since insects are often only capable of detecting and avoiding webs, after it appears that they are going to strike it (Turnbull 1960; Buskirk 1975; pers. obs.). If an insect is able to detect individual threads and alter its course to avoid a collision (or fly mistakenly into another sticky thread), it will probably do so because the thread is there and not because it may or may not be sticky. The elimination of "radii" from ASW traps could alter the flight behavior of small insects that are capable of flying through wider meshes in a way that is different than if they were present. Because the function of these devices is to intercept flying insects in nearly the same manner as spider webs, Chacon and Eberhard (1980) may be too harsh in their criticism of ASW's as mimics of spider webs. Even in illuminated areas, insects were only occasionally seen to avoid both spider webs and ASW's, and the capture rate for ASW traps was as high as or higher than that of the webs under observation. We would expect capture rates of ASW's to be lower than those of spider webs if the visibility of the traps affected their intended function. Consequently, while not being exact mimics of spider webs, ASW traps are reasonably effective sampling devices for flying insects in a forest understory. While some authors have discouraged their use (see Chacon and Eberhard 1980) and ASW's may not be suited for use in all environments, we feel that they can effectively sample the potential prey of many orb-weaving spiders better than conventional sampling methods (see Uetz and Biere 1981 for field comparisons).

A comparison of web catches with ASW's will reveal if the web of the spider contributes to dietary selectivity. Data from observations, and from web traps placed nearby while observations were being made, were analyzed using an index of dietary specialization—the

Table 1. Web selectivity (E_w) values for prey types and sizes caught in webs of *Micrathena gracilis*

	Caught in spider web		Caught in sticky trap		E_w
	No.	R_i	No.	P_i	
<i>Taxon</i>					
Diptera	89	.669	268	.355	+.307
Hymenoptera	20	.150	338	.448	-.498
Coleoptera	5	.038	48	.064	-.255
Homoptera	4	.030	43	.057	-.310
Thysanoptera	-	.000	21	.028	-1.00
Psocoptera	-	.000	11	.015	-1.00
Hemiptera	-	.000	8	.011	-1.00
Lepidoptera	-	.000	1	.001	-1.00
Other (Unident.)	-	.000	17	.023	-1.00
<i>Size mm</i>					
0-2	56	.475	600	.795	-.252
2-4	32	.271	138	.183	+.194
4-6	16	.136	13	.017	+.778
6-8	4	.034	2	.003	+.838
8+	10	.085	2	.003	+.932

"Electivity" index of Ivlev (1961): $E = r_i - p_i/r_i + p_i$ where r_i = proportion of item i taken, and p_i = proportion of item i available. Values for this index range from +1.0 (highly preferred) to -1.0 (least preferred). For this comparison, the catches of the artificial webs were assumed to estimate the proportions of prey available in each size class or taxon considered.

RESULTS

Of the 133 insects observed to strike webs, 118 stuck to the web for at least 3 sec. (for an initial web capture efficiency of 88.7%). Of these 118 insects, 66 were actively attacked by the spider, 44 were ignored, and 8 escaped before a "decision" was made. Of these 66 insects actively attacked, 54 were captured, 5 were rejected, and 7 escaped due to mishandling. A total of 38 insects escaped at some point in the predatory sequence (Fig. 1), leading to an overall web capture efficiency of 71.4% (HIT-ESCAPE/HIT \times 100).

Comparison of traps and webs indicate that the webs of *Micrathena gracilis* are selective, and show electivity for Diptera sized >2 mm (Table 1). However, the majority of insects hitting and then sticking to the web was quite small (<3 mm): 53% (70 of 133 hits) and 58% (67 of 116 sticks) respectively. Therefore, well over half of the

insects which encountered the web (and were thus available as potential prey items) were small insects containing very little biomass/insect.

Larger insects contain far more biomass per individual, but they are much rarer. Since the electivity index measures the degree to which prey are preferred in comparison to their availability, the results of the comparison between the web and the trap suggest that the web selectively retains larger prey. This conclusion is supported by the observation that escapes occurred in nearly the same proportion for all size classes except for the smallest and the very largest (Fig. 2). Escapes by very small insects (1–3 mm) can be attributed to almost instantaneous escape after contact with the web. It is possible that these insects were not flying very fast but were strong enough to pull free of the web before the chance of attack. On the other hand, 75% of the insects > 9 mm escaped before being attacked, with 50% of these insects escaping within 3 seconds of hitting the web. This is probably due to their faster flight velocities and strength (see Nentwig 1980).

As a consequence of web selectivity, *Micrathena* is presented with a preselected array of potential prey items to "decide" whether to attack. Within this array, the spiders were observed to attack a greater proportion of larger insects than smaller ones (Fig. 2). A comparison of prey taken by the spiders with those taken by the web shows evidence of greater selectivity (Table 2). The Ivlev index values are highest for Diptera in the middle range of size classes (4–8 mm). The frequency of insects attacked or ignored vs. insects sticking in each size class shows that *Micrathena* is not attacking (or ignoring)

Table 2. Spider selectivity (E_s) values for prey types and sizes caught by *Micrathena gracilis*

	Captured by spider		Caught in web		
	No.	R_i	No.	P_i	E_s
<i>Taxon</i>					
Diptera	41	.759	89	.669	+.670
Hymenoptera	10	.185	20	.150	−.567
Coleoptera	2	.037	5	.038	−.013
Homoptera	1	.019	4	.030	−.224
<i>Size (mm)</i>					
0–2	20	.370	56	.475	−.124
2–4	16	.296	32	.271	+.044
4–6	13	.241	16	.136	+.279
6–8	2	.037	4	.034	+.042
8+	3	.056	10	.085	−.206

insects in each size class with the same frequency in which they are encountered. A Kolmogorov-Smirnov test of the difference in the frequency distributions across size classes of those insects sticking to the web and those being attacked by the spider indicates a significant difference ($p < .001$), supporting a rejection of the null hypothesis of no selectivity. This spider is ignoring the smaller, more abundant insects sticking to the web and is preferentially attacking the larger yet rare insects.

DISCUSSION

The constraints on spider "decision-making" in the prey capture process involve a balance between the cost of handling of the prey item and the return in biomass from the investment of energy in its capture. Turnbull (1973) suggests that the size range of prey attacked by spiders is set at the lower end of the range by a minimum amount of biomass needed to "justify" the energy expended, and at the upper end of the range by limits to handling probability of escape, and danger to the spider. The profitability of prey capture by spiders will thus determine how much a spider will specialize on particular prey types. If among the prey available there are species which are easier to capture and/or subdue, or in some way are more likely to provide a high reward for the energy expended, they should be preferred over others (which should be ignored or rejected unless the hunger level dictates otherwise) (Charnov 1976). Riechert (in Riechert & Luczak 1982) has shown that *Agelenopsis* rejects a total of 20.8%, and ignores 11.3%, of all potential prey, based primarily on the profitability factors mentioned above. She also found that the majority of these "decisions" were made early in the prey capture sequence, and suggests that selection should favor discrimination among prey before much energy is expended in the capture process.

Micrathena appears to concentrate its efforts on larger size classes where the available biomass is the greatest, not the small size classes where the abundance of prey is the greatest. This species forages in an optimal manner in the long term sense (Dawkins 1986), by electing to attack the size classes and taxa that provide the spider with the most energetic reward, despite low availability. Even though the spider would appear to forage in a sub-optimal manner, by ignoring a disproportionately higher number of small prey, it is not necessarily omitting a large amount of biomass (<15%) from its diet by doing so (Nentwig 1985). It is probable that the spider consumes these insects at night when it takes down its web (if the insects do not escape during the

day). The spider may therefore reap this collective caloric benefit without actively attacking each small insect striking its web during the day.

By following the predatory sequence of *Micrathena gracilis* (Fig. 2), it is clear that throughout the sequence, the spider is presented with many more small insects than large insects. After the web has restrained an insect, the spider will either attack it or ignore it. It has been shown that the spider attacks insects > 3 mm with a significantly higher frequency than it does those < 3 mm, which are ignored most of the time. Similar results were seen in *Micrathena schreibersi*, a neotropical congener (Shelly 1984). The term "ignore" implies that the spider actually makes a choice of what it attacks, which is what is implied in this study, and has been used by other arachnologists (e.g. Olive 1980; Riechert and Luczak 1982; Shelly 1984). During the course of observations, spiders did appear to make a choice of whether or not to attack certain insects, most probably based on some sort of vibrational stimuli. For example, the spider was often seen orienting toward the impact area of a small insect with the web, plucking the radii in that area, and even advancing a few millimeters toward the insect, but not attacking it. The impact of the insect may have been enough of a vibrational stimulus to initiate the attack sequence, but the lack of vibration after impact indicated either a very small prey item or no prey item. Suter (1978) found that the impact stimulus was important in initiating the attack behavior of *Cyclosa turbinata*, another forest-dwelling orb-weaver. This particular species may be capable of detecting the mass of an insect by its impact vibration, which could be, according to Suter, a mechanism for discerning the insect's relative food value. This same mechanism could be operating in *Micrathena*.

Riechert and Luczak (1981) suggest that three parameters regarding profitability should be important in the spider's decision to consume (attack) or ignore the prey item: prey type, prey size, and level of hunger. Observations of other species indicate that orbweavers are able to discriminate between prey and alter their attack behavior accordingly (Eberhard 1967; Robinson 1969; Robinson, Mirick, and Turner 1969; Robinson and Olazarri 1971; Robinson and Mirick 1971; Robinson & Robinson 1973, 1976) allowing them to secure prey in such a way as to prevent quick escapes and/or minimize the risk of injury. Most of the potential prey of *Micrathena* is small Hymenoptera and Diptera (as seen in availability estimates in Table 1), and they pose little threat to the spiders. *Micrathena* exhibits the more primitive "bite-wrap" behavior pattern (Robinson et al. 1969),

which suggests that it should be more efficient in attacking fast-escaping but relatively harmless prey. Prey size is probably a more important criterion in prey selectivity for such a species than is prey type. The hunger level of the spider may also play an important role in what the spider may choose to attack, but it is a difficult parameter to control in observational field studies such as this. Spiders are often subjected to severe food shortages (Olive 1982) and may switch from being a specialist to a generalist, i.e. accept a less preferred prey item due to the paucity of preferred prey types (Emlen 1966; Schoener 1969, 1971; Pulliam 1974; Lacher et al. 1982).

The degree of selectivity shown by *Micrathena gracilis* is surely not as precise as many prey specialists (see Stowe 1986). However, given that any specialization should be risky for a spider with its attributes, this prey selectivity must pay off in providing this species with an apparently adequate diet.

SUMMARY

The prey of a common deciduous forest orb-weaver, *Micrathena gracilis* (Walckenaer), was compared with potential prey sampled by artificial sticky web traps. Comparison of traps and webs indicated that webs of *Micrathena* are selective, showing selectivity for Diptera sized greater than 3 mm, even though the majority of prey hitting webs and in traps are much smaller. Spiders also showed selectivity in attacking larger dipteran prey, and ignoring the majority of tiny insects (< 3 mm) stuck in their webs. Prey specialization seen in *Micrathena* appears based primarily on insect size, and is likely related to the profitability (energetic reward) of larger Diptera as prey.

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